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THE TAXONOMY OF VACCINIUM § OXYCOCCUS

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In Eastern North America, both Fernald (1950) and Gleason (1952) recognized but two specific entities in *Vaccinium* § *Oxycoccus* (Hill) Koch, namely, *V. oxycoccus* L., the small cranberry and *V. macrocarpon* Aiton, the large cranberry. However, taxonomists who have dealt with the group in the boggy places of the circumboreal taiga have, as a rule, split *V. oxycoccus sensu lato* into two or more segregate species, for example, *V. oxycoccus sensu stricto* and *V. microcarpum* (Turcz ex Rupr.) Schmal. (Tutin et al., 1972); *Oxycoccus* quadripetalus Gilib and *O. microcarpus* Turcz ex Rupr. (Bobrov & Bush, 1967); *O. microcarpus* and *O. palustris* Pers. (Polunin, 1959); *O. microcarpus*, *O. quadripetalus*, and *O. ovalifolius* (Michx.) Porsild (Scoggan, 1979; Porsild, 1938).

The basis for this splitting of *Vaccinium oxycoccus* s.l. into segregates stemmed from the discovery that this species is comprised of populations which have different chromosome numbers: some are diploid, 2n = 24 (Hagerup, 1940; Darrow, et al., 1944; Löve & Löve 1956; and Jorgensen, et al., 1958); others tetraploid, 2n = 48 (Hagerup, 1940; Darrow, et al., 1944; Hara, 1956; Jorgensen, et al., 1958; Löve & Löve 1966; and Pojar, 1974); and still others are hexaploid, 2n = 72 (Hagerup, 1928; Tischler, 1934; Rohweder, 1937; Newcomer, 1941; and Jorgensen, et al., 1958). However, gross morphological characters which run parallel to these ploidy levels have been difficult to find. Pedicel indumentum in conjunction with leaf dimension have been used most frequently to separate the

[&]quot;I will not address the question of generic rank for Oxycoccus at this time but will follow the classification of Sleumer (1941) and Stevens (1969).

taxa Reference V. microcarpum character V. oxycoccus s.s. O. ovalifolius O. quadripetalus O. microcarpus O. palustris Porsild (1938) ± glabrous pedicels ± glabrous pubescent Porsild & Cody (1979) puberulent glabrous Tutin et al. (1972) puberulent glabrous Polunin (1959) ± glabrous pubescent Ohwi (1965) puberulent usually glabrous Bobrov & Bush (1967) ± pubescent glabrous Porsild (1938) below the middle locations of usually below the Polunin (1959) pedicel bracts below, at, or above middle the middle Ohwi (1965) below the middle near the middle Bobrov & Bush (1967) above the middle below the middle Bobrov & Bush (1967) densely hairy filaments Tutin et al. (1972) puberulent

cranberries.

Comparison of morphological characters used by various authors to differentiate among the small

leaf length	6-10 mm	2-6 mm	6-8 mm	Porsild (1938)
ioui iongui	4-9 mm	2-4 mm	O O IIIII	
	6-10(-15) mm			Porsild & Cody (1979)
		3-8 mm		Tutin et al. (1972)
	2-10 mm	2-6(-8) mm		Polunin (1959)
	5-12 mm	3-6 mm		Ohwi (1965)
	8-16 mm	3-7.5 mm		Bobrov & Bush (1967)
leaf width	2-5 mm	1.5-2 mm	2-3 mm	Porsild (1938)
	3-6 mm	1-2.5 mm		Tutin et al. (1972)
	1.5-5 mm	1-2(-3) mm		Polunin (1959)
		2-2.5 mm		Ohwi (1965)
	3-6 mm	1-2.5 mm		Bobrov & Bush (1967)
berry diameter	8-12 mm	5-7 mm	10-12 mm	Porsild (1938)
	8-14 mm	5-10 mm		Porsild & Cody (1979)
	(6)8-10(-15) mm	5-8 mm		Tutin et al. (1972)
	7-13 mm	5-7(-8) mm		Polunin (1959)
	10 mm	6-7 mm		Ohwi (1965)
	10-18 mm	5-10 mm		Bobrov & Bush (1967)
chromosome	2n = 48	2n = 24		Tutin et al. (1972)
number	2n = 48	2n = 24	2n = 48	Darrow et al. (1944)

diploid *V. microcarpum* from the tetraploid *V. oxycoccus* s.s. (Table 1). The hexaploids (2n = 72) occur infrequently and are thought to be sterile hybrids between *V. oxycoccus* and *V. microcarpum* (Hagerup, 1940; Camp, 1944). But as Table 1 shows, these characters (as interpreted by the various authors) do not unerringly separate the diploids from the tetraploids nor are pedicel indumentum and leaf dimensions invariably correlated: there are plants with glabrous pedicels which have the leaf size of *V. oxycoccus* s.s. and these have been referred by Porsild (1938) to *O. ovalifolius*; and then there are those plants which have pubescent pedicels and very small inrolled leaves and which have been referred to *O. palustris* ssp. *microphyllus* (Lge.) Löve & Löve, or by Camp (1944) to the "microcarpoid" phase of *O. quadripetalus*.

In her study on the variability of several vegetative and inflorescence characters in 50 Vaccinium oxycoccus specimens gathered from six bogs near Durham, New Hampshire, Rodrigues (1963) found that stem color varied from light brown to black; that leaf width varied from 1 to 4 mm and length varied from 3 to 10 mm and had mean dimensions of 2 ± 0.5 mm $\times 6\pm1$ mm which is interesting insofar as these values fall just at the boundary between Porsild's (1938) concept of V. microcarpum and V. oxycoccus (see table 1); that the leaf blades of several specimens were flat, others slightly revolute, and yet others revolute (conditions she attributed to relative exposure of the plants); and that the leaf apices were mostly pointed and that only a few had slightly rounded apices. She also showed that a significant source of the leaf variation described above arose from between plants rather than within plants.

Furthermore, Rodrigues (1963) described all the pedicels as pubescent, bearing a pair of green or red bracts (a few pedicels had none at all) whose shape varied from long and narrow to leaf-like to very small scales. Pedicel number varied from one to four and in 21 specimens arose from the axils of the uppermost reduced leaves, thereby forming an apparent terminal cluster (figure 1); in the remainder, however, the pedicels were in the axils of the lowermost reduced leaves of a normal leafy branch: a condition I have also observed in Cape Breton, Nova Scotia (figure 8) and which results in an inflorescence type usually associated with *Vaccinium macrocarpon*.

Indeed, as Boivin (1967) has noted, "the diagnostic characters [for the small cranberry taxa] are not quite constant and various recombinations of characters occur here and there. He who would here accept two species will eventually be led to accept four, then perhaps eventually eight...!"

Another difficulty arises whenever herbarium specimens are examined. A sheet of several fragments (see figures 1, 2, 3, especially their annotations) each bearing one or two pedicels, several of which may be quite glabrous, others quite puberulent, may be the result of a mixed gathering; a likely event since, according to Bobrov & Bush (1967) Oxycoccus microcarpus often occurs with O. quadripetalus in boreal peat bogs.

Nonetheless Camp (1944) argued that diploid *Vaccinium micro-carpum*, which is found in Iceland, Europe, Asia, and northwestern North America but is unknown from Labrador and Greenland, is quite homogeneous and is distributionally disjunct from its sister group *V. macrocarpon*.

Furthermore, according to Camp (1944) Oxycoccus quadripetalus is a mixture of tetraploid hybrids and their segregates which resulted from the contact O. microcarpus made with V. macrocarpon when it migrated southward in response to the advancing Pleistocene ice sheets.

The purpose of this paper is to test Camp's hypothesis, that in Vaccinium § Oxycoccus there are in fact two rather homogeneous diploid taxa, V. macrocarpum and V. microcarpum respectively, and a tetraploid-hexaploid population comprising a heterogeneous assemblage of hybrids and their segregates, using numerical and experimental taxonomic techniques.

MATERIALS AND METHODS

To assess morphological discontinuity 26 likely cranberry habitats, mostly in eastern North America, such as bogs, raised bogs, boggy barrens, high moors, wet meadows, headlands, and low tundras were surveyed between 1969 and 1980 (for geographical details see Appendix). If, after a careful search, a site had more than ten cranberry colonies present, three 200 m grid lines were laid out in a random fashion. At every 10 m, the nearest cranberry plant was flagged and identified by number. If there was no plant within 1 m of the 10-m mark of the tape, the point was declared empty. For every 10 plants flagged, three were drawn at random and permanently tagged so that they could be revisited during the flowering

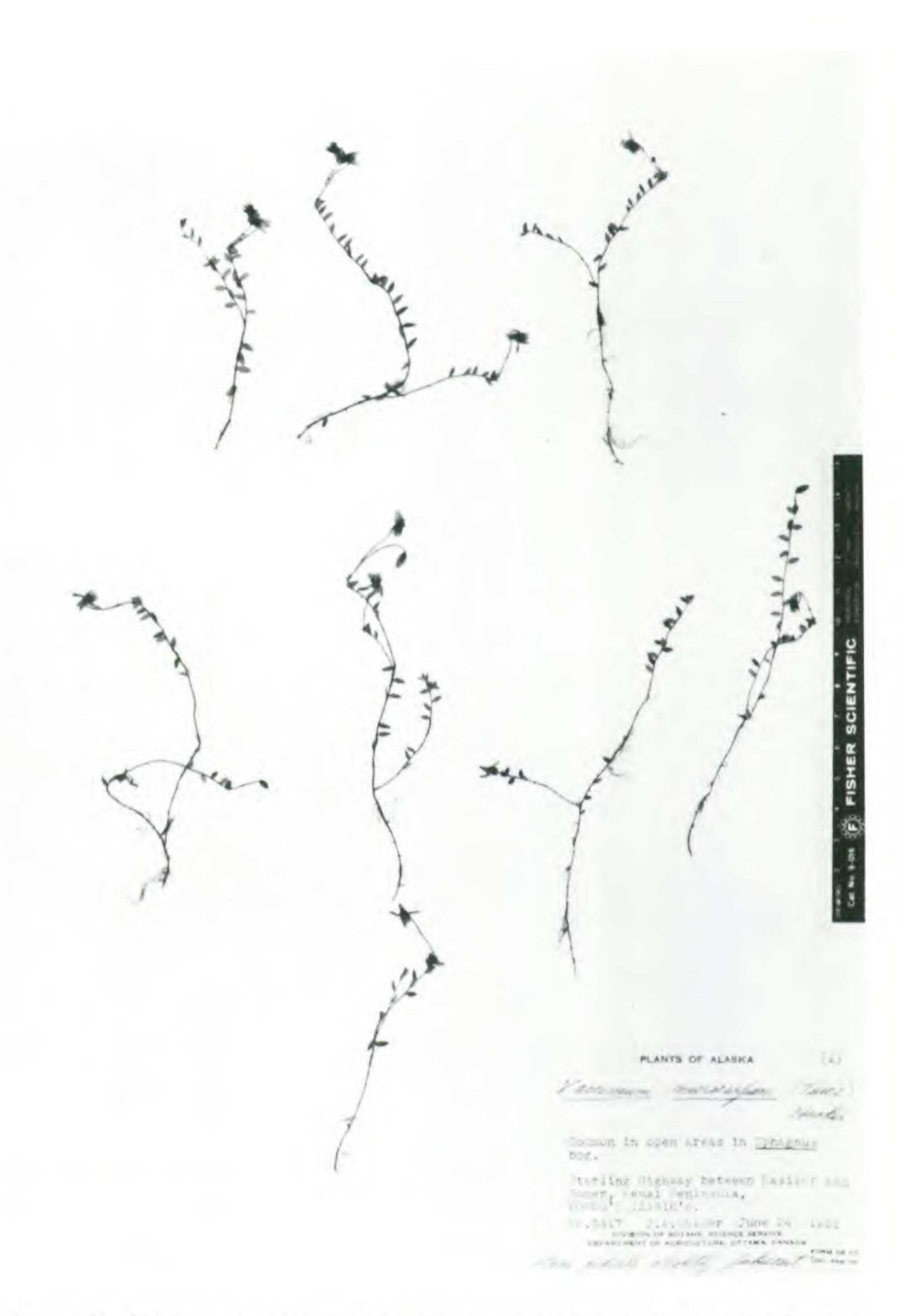


Figure 1. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in V. oxycoccus.

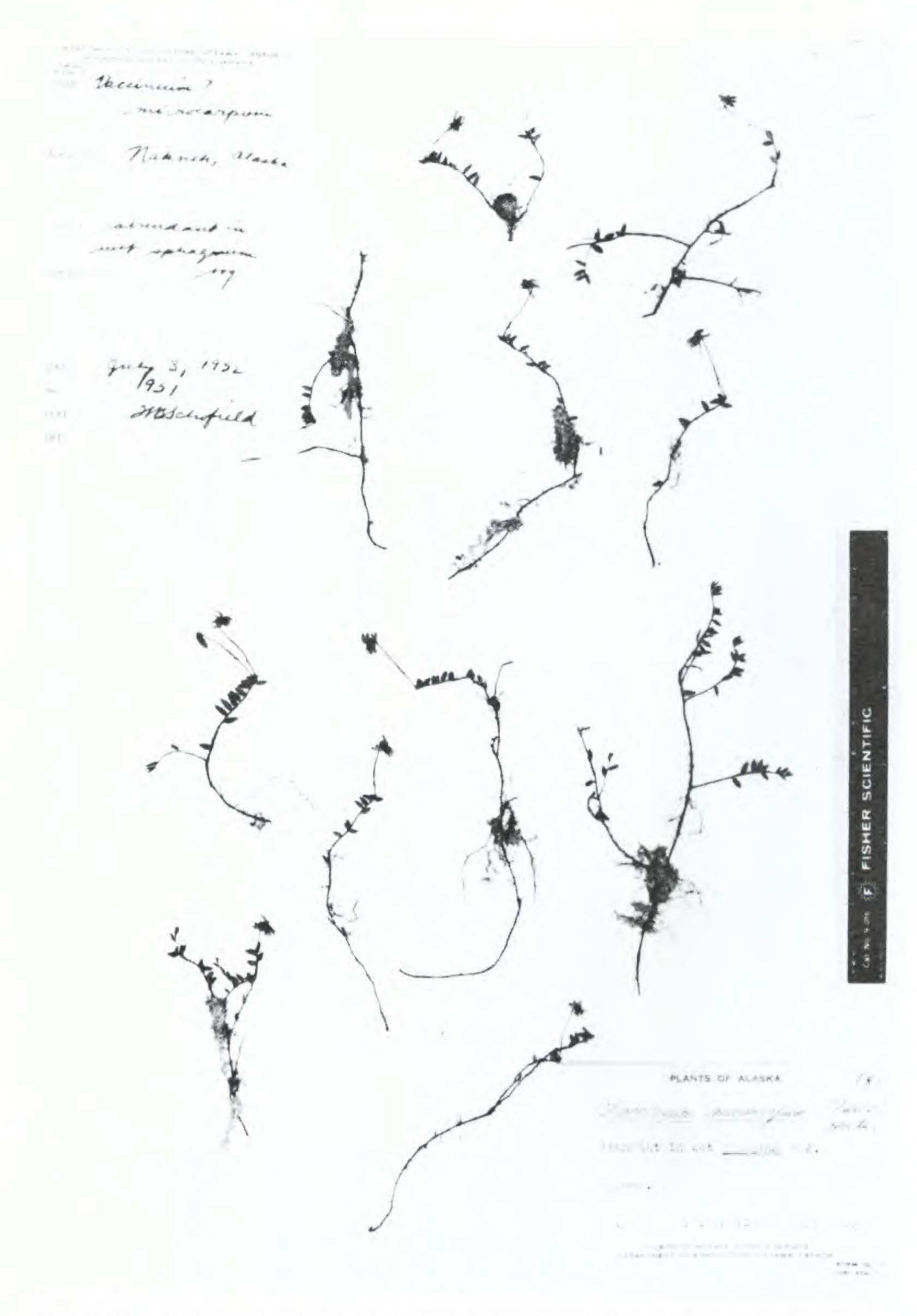


Figure 2. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

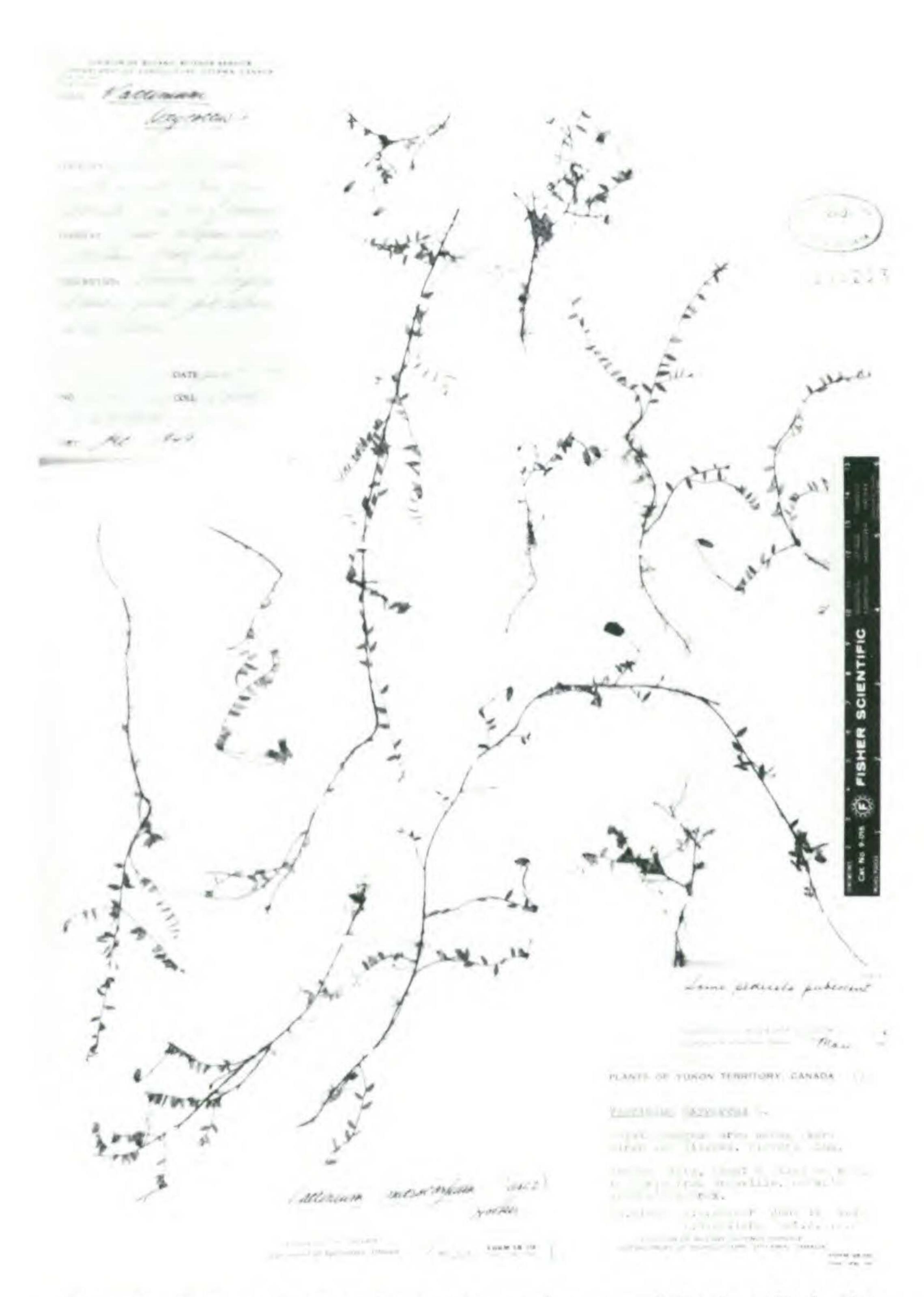


Figure 3. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in V. oxycoccus.

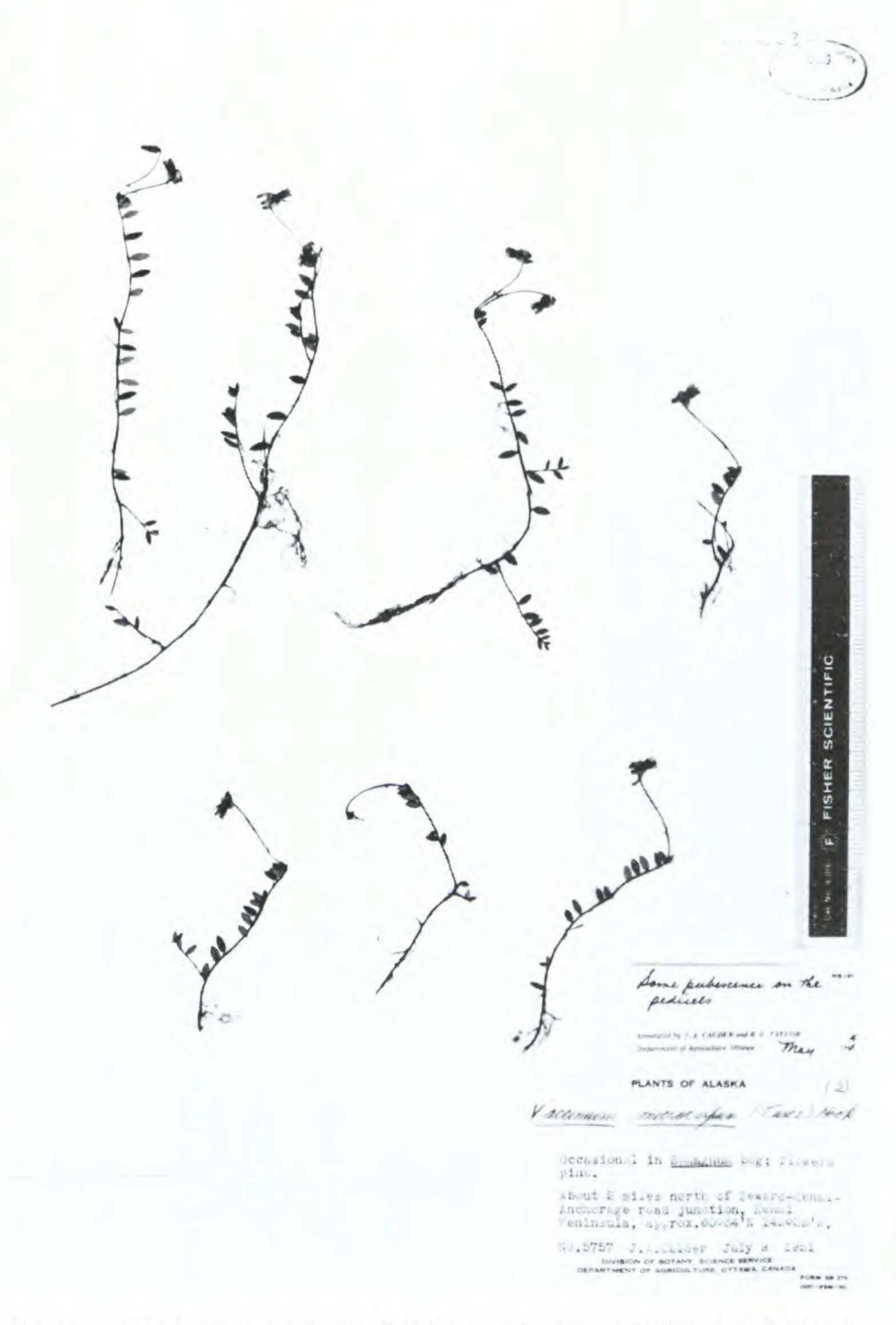


Figure 4. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in V. oxycoccus.



Figure 5. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in V. oxycoccus.

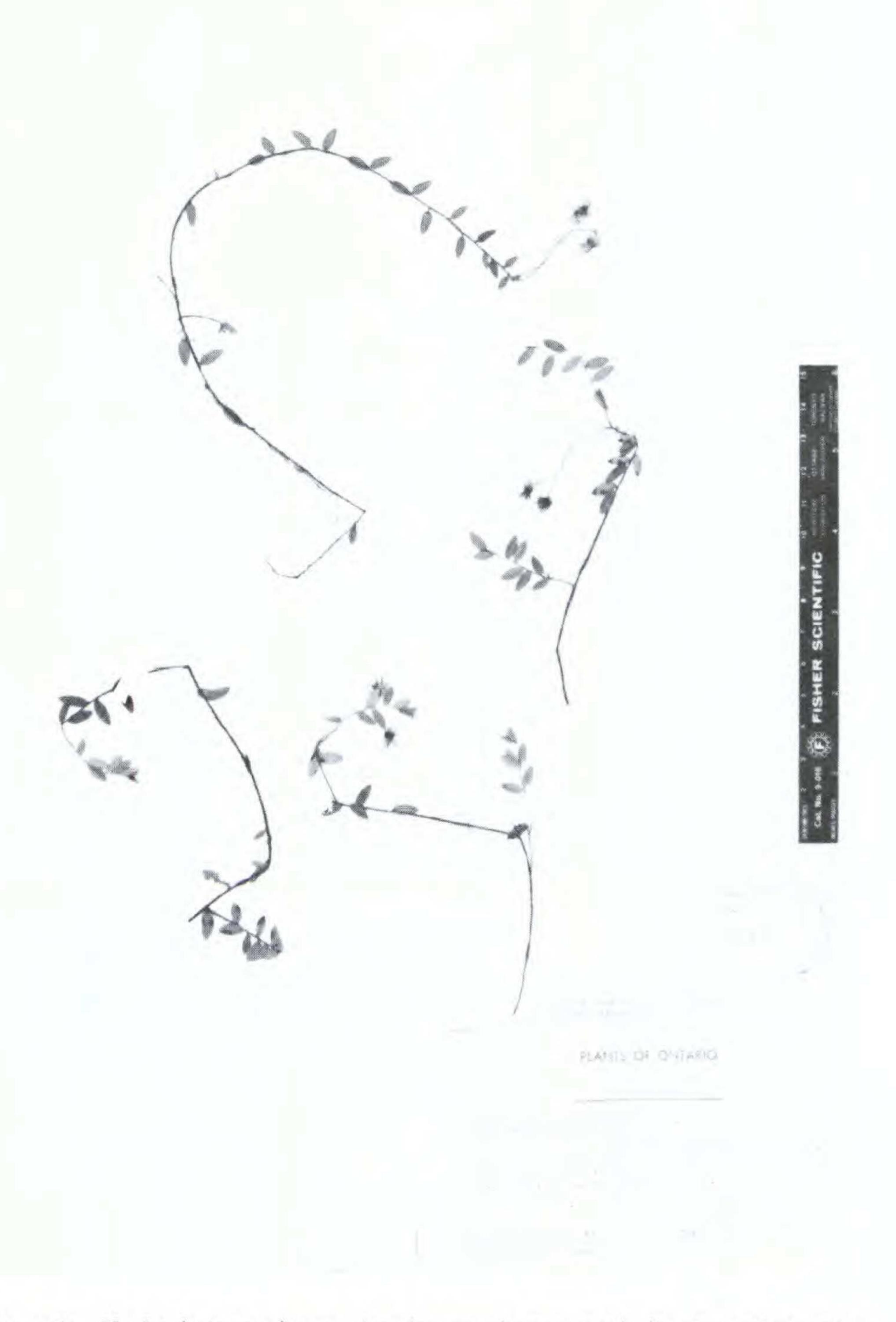


Figure 6. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

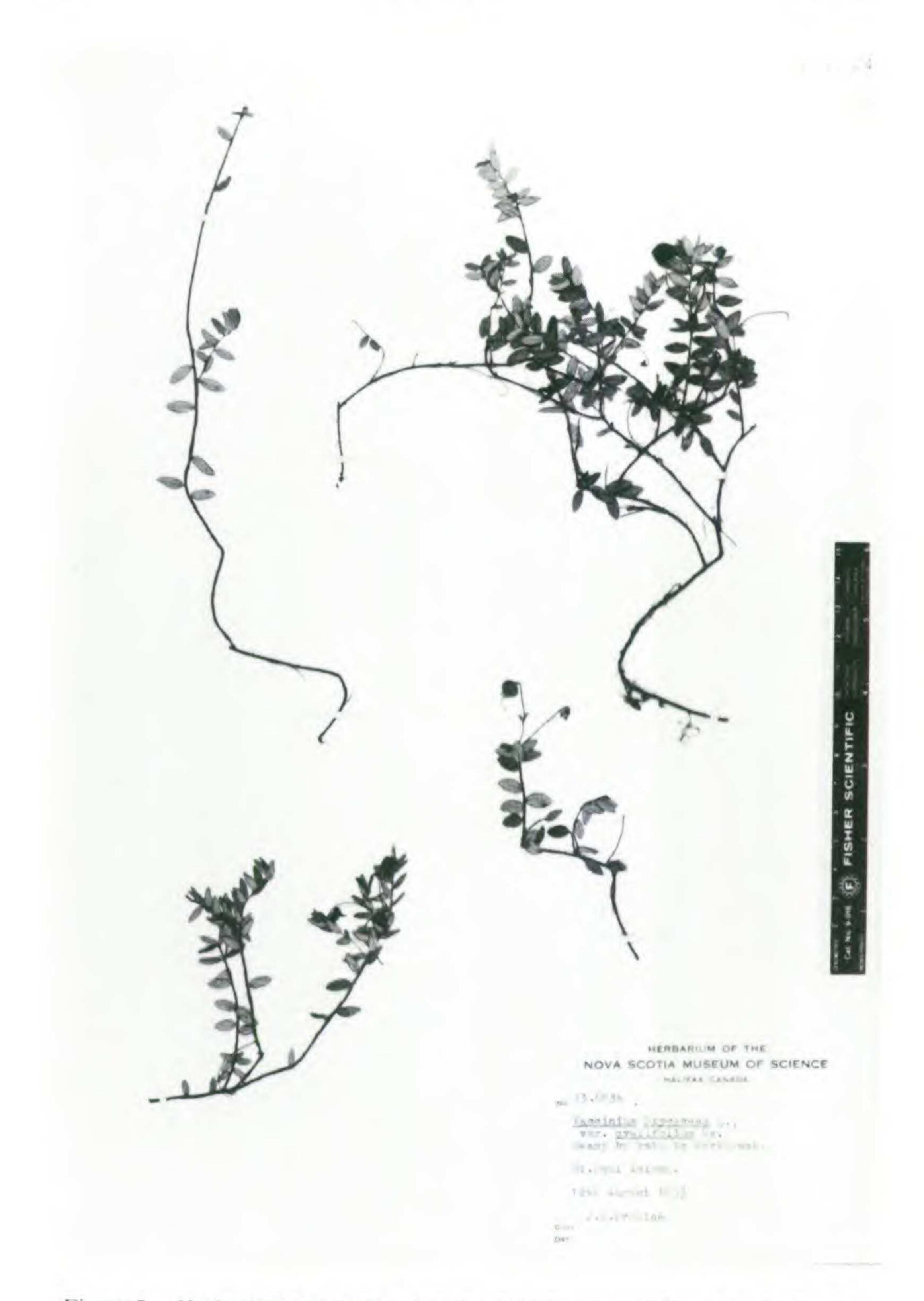


Figure 7. Herbarium specimens showing continuous variation in pedicel pubescence and leaf size in *V. oxycoccus*.

and fruiting season for at least two reproductive bouts. Flowers, fruits and a few mature vines from each number were collected and dried. Voucher specimens are at ACAD². Soil samples were taken and ecological habitat notes were made for each collection. In addition, a few, usually five or more, berries were harvested from each plant so that germination trials could be carried out and the growth morphology of the seedlings compared with that of the female parent.

Table 2. Morphological comparison between selected attributes of V. macrocarpon and V. oxycoccus

character	V. $macrocarpon$ (n = 136)	V. $oxycoccus$ (n = 246)	
length of flowering shoot (cm)	5.5 ± 3.4	2.3 ± 0.8	
width of pedicel bracts (mm)	1.3 ± 0.4	0.4 ± 0.2	
leaf width (mm)	3 ± 0.5	2 ± 0.7	
leaf length (mm)	8 ± 1.3	5 ± 1.5	
ratio w:l	1:2.66	1:2.50	
leaf shape	narrowly elliptic	ovate	
berry diameter (mm)	12 ± 2	9 ± 2	
large seeds/berry	17 ± 8	8 ± 5	
seed weight (mg/100)	91 ± 28	68 ± 17	

Next, 114 dried specimens were scored for the following 12 features: (1) length of fertile shoot; (2) width of bracts on pedicel at anthesis; (3) pedicel indumentum (pubescent, intermediate, or glabrous); (4) calyx lobes (pubescent at the tip or glabrous); (5) stamen filaments (pubescent, pubescent along the margins, or glabrous); (6) leaf blade (revolute, intermediate, or flat); (7) mean leaf width; (8) mean leaf length; (9) leaf length to width ratio; (10) leaf shape (ovate, narrowly ovate, or narrowly elliptic); (11) indumentum in

²Acronyms follow Index Herbariorum (Holmgren & Keuken, 1974).

twigs of the current season (puberulent or glabrous); (12) berry diameter.

However, since my sampling space was restricted to northeastern North America, where according to Camp (1944) and Porsild (1938) V. microcarpum is absent, I decided to augment the basic data matrix described above with selected herbarium specimens (cited under specimens examined) from the Northwest Territories where according to Porsild & Cody (1979) V. microcarpum is frequent and V. oxycoccus is rare, known to occur only from a few muskegs adjacent to the Liard and upper Mackenzie Rivers.

Furthermore, because my sampling procedure was unbiased towards the inclusion of rare "morphs", I also added several herbarium specimens which had been identified as *Vaccinium oxycoccus* var. *microphyllum* or *V. oxycoccus* var. *intermedium* or *V. oxycoccus* var. *oxycoccus* var. *ovalifolium* or looked somewhat dubious.

Whenever a herbarium specimen had a missing feature (e.g. no ripe berries) I would dub in the appropriate value using the Flora of the region where the plant had been collected: thus if fruit was absent from a Keewatin specimen which had been referred to V. microcarpum, I would check Porsild & Cody (1979) for berry size and use their median value for the data matrix.

After the discretely scored characters had been converted to multistate characters, a non-metric coefficient $S_{SM} = \frac{M}{m+u}$ was calcuculated for each pair of specimens; then the similarity coefficients were sorted by way of an unweighted pair-group clustering method based on arithmetic averages (UPGMA). Sneath & Sokal (1973, p. 132 & p. 230) furnish details of these procedures.

Since dendrograms are only useful at depicting nearest neighbour relationship and are less reliable at the higher internodes, i.e. at the group level, I also subjected the data matrix to Principal Component Analysis. In this procedure individuals are ordered along uncorrelated axes, while variation in all characters among all the individuals is considered simultaneously (Sneath & Sokal, 1973, pp 245-247). Any major groupings in the sample data are elucidated through this sorting technique. In summary then, UPGMA is very useful in describing the relationship between pairs of individuals, while PCA detects major patterns in the data.

For the actual processing, I used the numerical taxonomy system (NT-SYS) written by F. J. Rohlf, J. Kishpaugh and D. Kirk (1974,

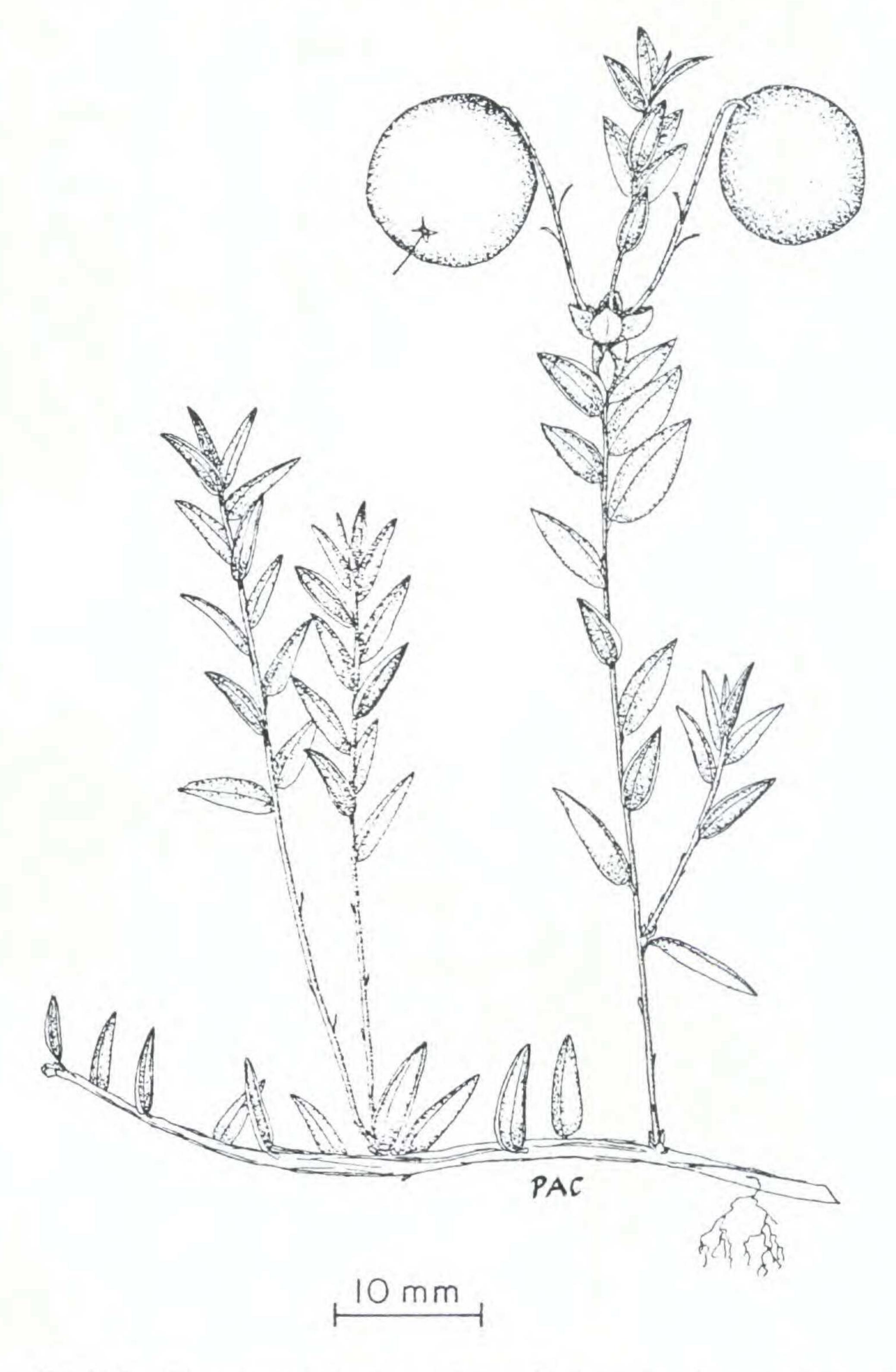


Figure 8. V. oxycoccus bearing a "normal" flowering shoot (Vander Kloet 419673).

State University of New York, Stony Brook). In the PCA routine, however, the character states were not converted to multistate characters but were read as continuous, which is justifiable since all the characters scored were ordered.

Once the germinated seedlings had had their chilling requirements fulfilled in a cold frame, and had begun to produce new shoots and/or flower buds, several actively growing stem tips or developing floral primordia were fixed, stained, and squashed according to a procedure described by Hall & Galletta (1971) so that the chromosome number for a number of plants might be ascertained.

Finally, to substantiate distribution data, herbarium specimens from North America were examined at A, ACAD, ALTA, BM, CAN, DAO, GH, K, LINN, NEBC, NHA, NY, NYS, PH, QK, TRT, UAC, UBC, and V.

RESULTS

In the first dendrogram (figure 9), which is based on field data only, initial separation occurred at a similarity coefficient of 0.38 and resulted in the formation of two groups: one whose members fell within the circumscription of *Vaccinium macrocarpon* and the other V. oxycoccus sensu Fernald (1902 & 1950) and Rodrigues (1963). Inspection of some of the smaller clusters within these specific groups shows that the V. macrocarpon cluster contains more variability than the V. oxycoccus. Thus OTU's 68, 57, 75, 69, 63 and 66 form a subgroup of \pm glabrous members in V. macrocarpon, whilst OTU's 79, 54, 82, 71, 81, 78, 55, 62, 58, and 65 form a subgroup of rather robust and pubescent plants.

When the herbarium specimens were added to the matrix, initial separation occurred at a similarity coefficient of 0.35 (figure 10) and again resulted in the formation of two groups, namely *Vaccinium macrocarpon* and *V. oxycoccus* s.l. OTU 10 was the only specimen added to the *V. macrocarpon* cluster; this specimen had been misidentified as *V. oxycoccus*. Within the *V. oxycoccus* cluster several new groups appeared: the most noteworthy of these being OTU 6, a specimen which can be referred to *Oxycoccus ovalifolius* since it has glabrous pedicels and large flat ovate leaves, and OTUs 2, 3, 44, 9, and 43, a mixture of specimens which had been identified as *V. microcarpum* and *V. oxycoccus* var. *microphyllum*.

The remaining *V. oxycoccus* var. *microphyllum* specimens (OTU's 45, 42, 46, 41, 47, and 7) were linked more closely to *V. oxycoccus* per se.

Table 3. Difference in germination of autumnal and vernal collections of Vaccinium § Oxycoccus seeds.

Collection Time	taxa	samples	number of seeds	% germination	Radicle emerges days	Dicotyledons	True leaves days
Autumnal harvest	V. oxycoccus	19	1067	21	19 ± 4	30 ± 3	38 ± 7
	V. macrocarpon	17	2434	5	26 ± 10	38 ± 12	47 ± 14
Vernal harvest	V. oxycoccus	18	1057	92	10 ± 2	19 ± 1	24 ± 3
vernal marvest	V. macrocarpon	19	2082	52	9 ± 1	19 ± 2	25 ± 2

Note: \pm = one standard deviation.

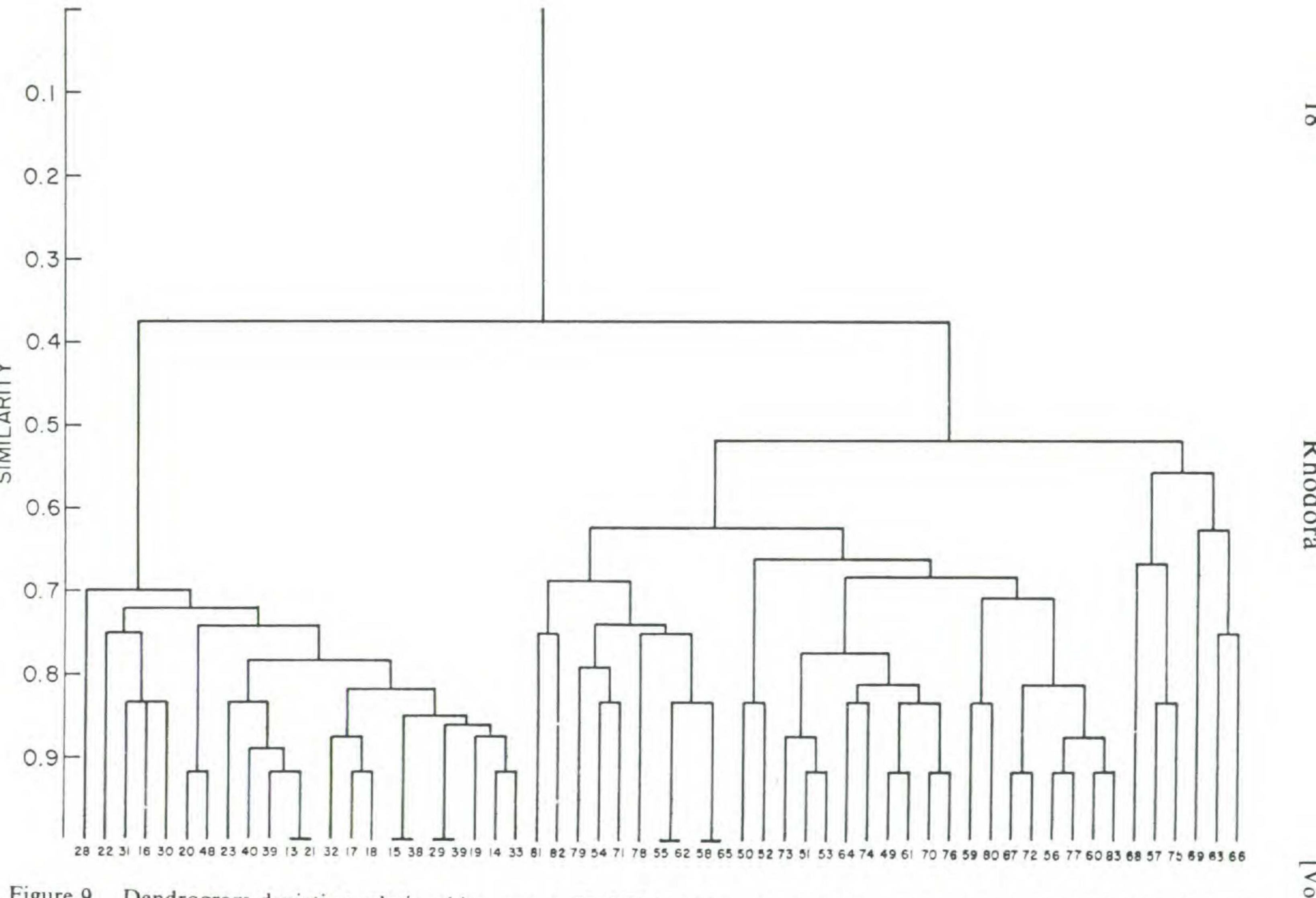


Figure 9. Dendrogram depicting relationships among 57 OTU's of Vaccinium § Oxycoccus specimens from 25 collecting sites in North America. (Details in text.)

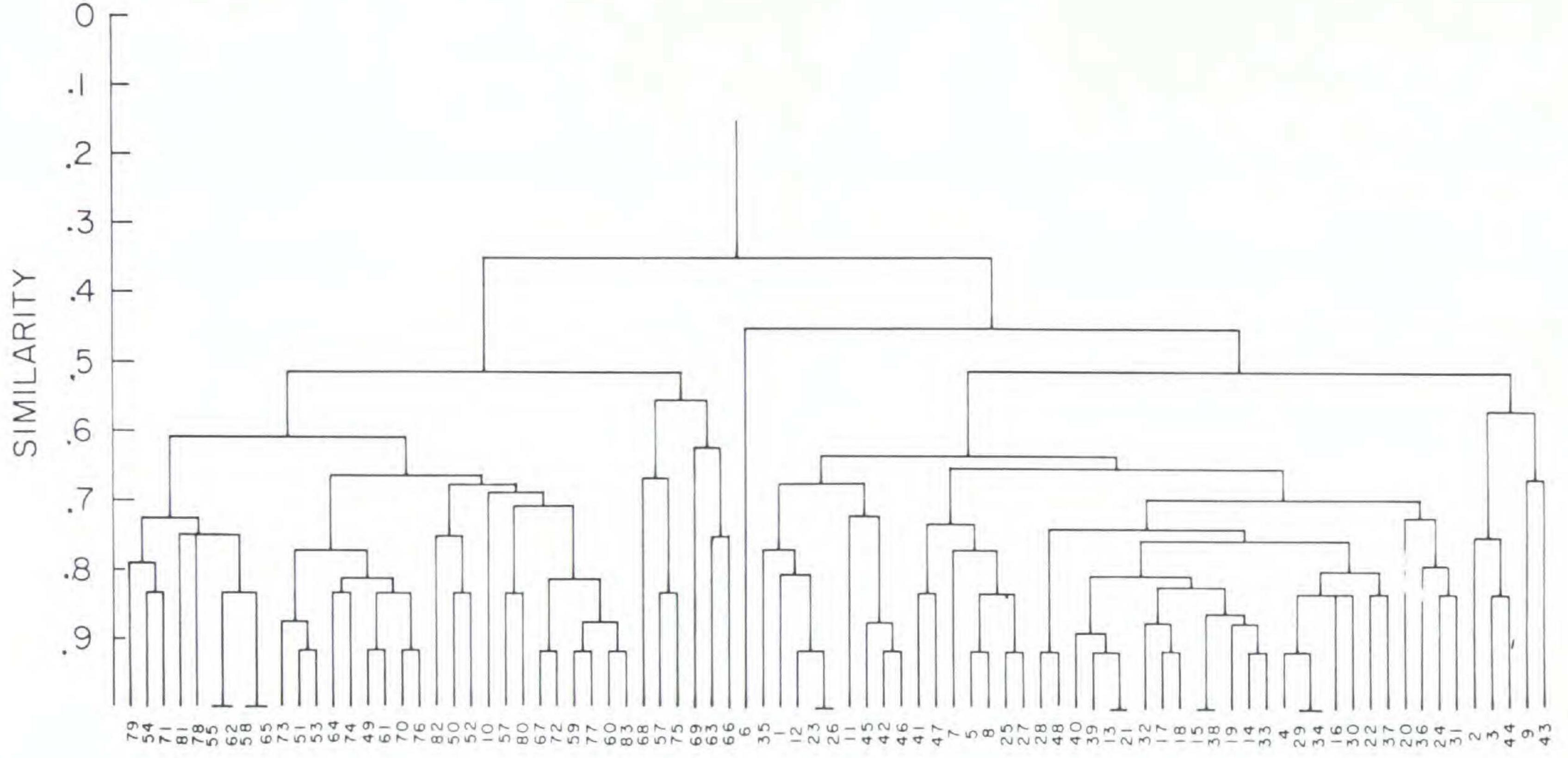


Figure 10. Dendrogram depicting relationships among 83 OTU's of Vaccinium § Oxycoccus based on both field and herbaria collections. (Details in text.)

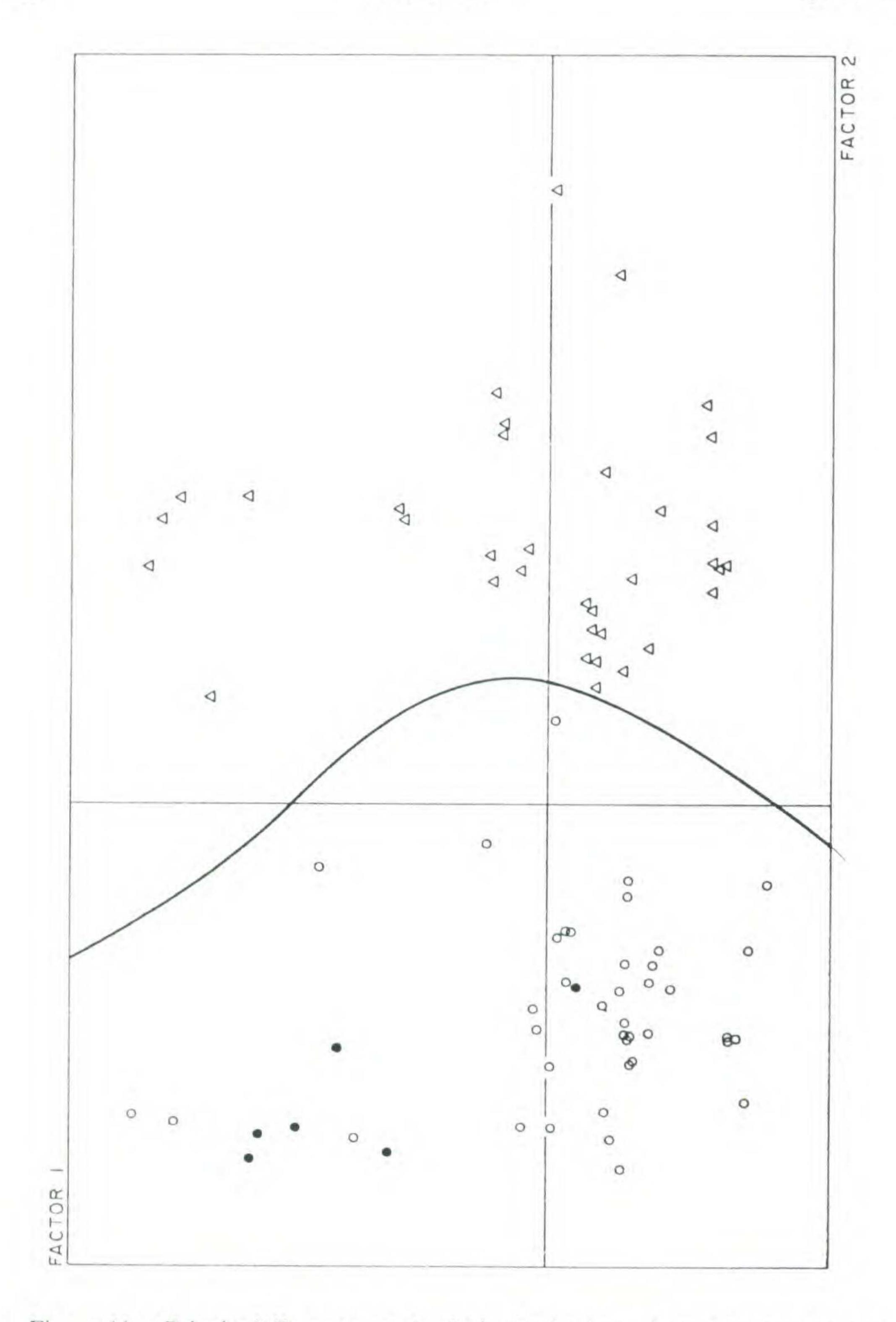


Figure 11. Principal Component Analysis. Projection of the first two factors. (Details in text.) Vaccinium oxycoccus on concave side of curve, V. macrocarpon outside curve. Triangles—V. macrocarpon; Open circles—V. oxycoccus s.s.; Closed circles—"V. microcarpum".

In the Principal Component Analysis (figure 11), the first two factors accounted for 64% of the variance. Two major clusters were delimited: Vaccinium macrocarpon and V. oxycoccus s.l. respectively. In the V. oxycoccus cluster OTU 6 (a specimen which had been identified as V. oxycoccus var. intermedium) occupies an isolated position. The specimens identified as V. microcarpus and V. oxycoccus var. microphyllum are again confounded and form (with the exception of OTU 47) a loose aggregate distinctly separated from the central constellation. Similarly, in the V. macrocarpon group the ± glabrous plants occupy a somewhat isolated position.

In short, the numerical analyses suggest that the *Vaccinium macrocarpon* cluster contains as much variability as the *V. oxy-coccus* group; they do not lend support to the notion that *V. oxy-coccus* s.l. contains discrete morphological taxa that reflect ploidy level. Furthermore, at the phenetic level at least, Camp's (1944) hypothesis that *V. macrocarpon* and *V. microcarpum* are relatively homogeneous taxa (i.e. contain relatively little variability) and that *V. oxycoccus* s.s. is a heterogeneous assemblage could not be substantiated.

To recognize the "microcarpus-microphyllus" group isolated in the Principal Component Analysis as a separate taxon would confuse the very issue it was designed to clarify: that the tiny leaved, largely glabrous, diploid populations in *Vaccinium oxycoccus* s.l. are morphologically distinct from the tiny leaved, somewhat puberulent, tetraploid populations. Moreover any major herbarium holding will have sufficient specimens on hand so that a continuous series from the very small delicate plants to those which are quite robust can be compiled (figures 1-7). However, plants at either end of this morphological spectrum are much more common in the herbaria than in the field.

Mixed gatherings on a single herbarium sheet occur (figure 12), but this condition is usually readily identifiable using uniformity of leaf size and shape as a guide. Therefore specimens such as in figures 1-4 are most likely single gatherings which exhibit variability in pedicel indumentum, thereby indicating that perhaps pedicel indumentum is an unreliable diagnostic feature.

Furthermore, although much has been made of inrolled leaves in *Vaccinium oxycoccus* in both descriptions and diagnostic keys, this feature, as Rodrigues (1963) has implied, is quite plastic. I have



Figure 12. Herbarium collection containing more than one vine of V. oxycoccus.

transplanted vines with revolute leaves from exposed hummocks to the shady side of black-spruce clumps and to terraria in the greenhouse and in both places the next set of innovations had flat leaves. Moreover, seedlings, greenhouse grown from open pollinated berries gathered from *V. oxycoccus* plants with strongly revolute leaves, produced quite flat leaves during the winter which became progressively more inrolled as the seasons progressed.

Chromosome counts revealed no surprises: collections of *Vaccinium macrocarpon* pollen mother cells from Nova Scotia and Ontario were consistently diploid (n = 12) and all pollen mother cells of V. oxycoccus from Nova Scotia, Quebec and Ontario were consistently tetraploid (n = 24). Provenance of plants from which counts were made are marked with an asterisk in the appendix of collecting sites. Vouchers are at ACAD.

In fine, these analyses suggest that $Vaccinium \$ Oxycoccus consists of two rather heterogeneous groups, discriminated primarily on the basis of size (figure 11 and table 2), one of which fits into V. macrocarpon Aiton and the other into V. oxycoccus L. That these clusters ought to be recognized at the species level is further enhanced by the lack of crossing success between the groups. In the areas of sympatry, the groups are temporally separated by two to three weeks at anthesis as well; for example, in Nova Scotia V. oxycoccus blooms on the 27th of June \pm 13 days and V. macrocarpon on the 19th of July \pm 9 days. Similar differences in the time of anthesis were observed by Bell & Burchill (1955), who also found that in the resting stage, V. oxycoccus bract, sepal, and stamen primordia are differentiated only, there is no sign of stamen and carpel primordia; whilst in V. macrocarpon the stamen and carpel primordia show some signs of differentiation.

TAXONOMY

Vaccinium § Oxycoccus (Hill) Koch, Fl. Germ. and Helv. 474. 1837.

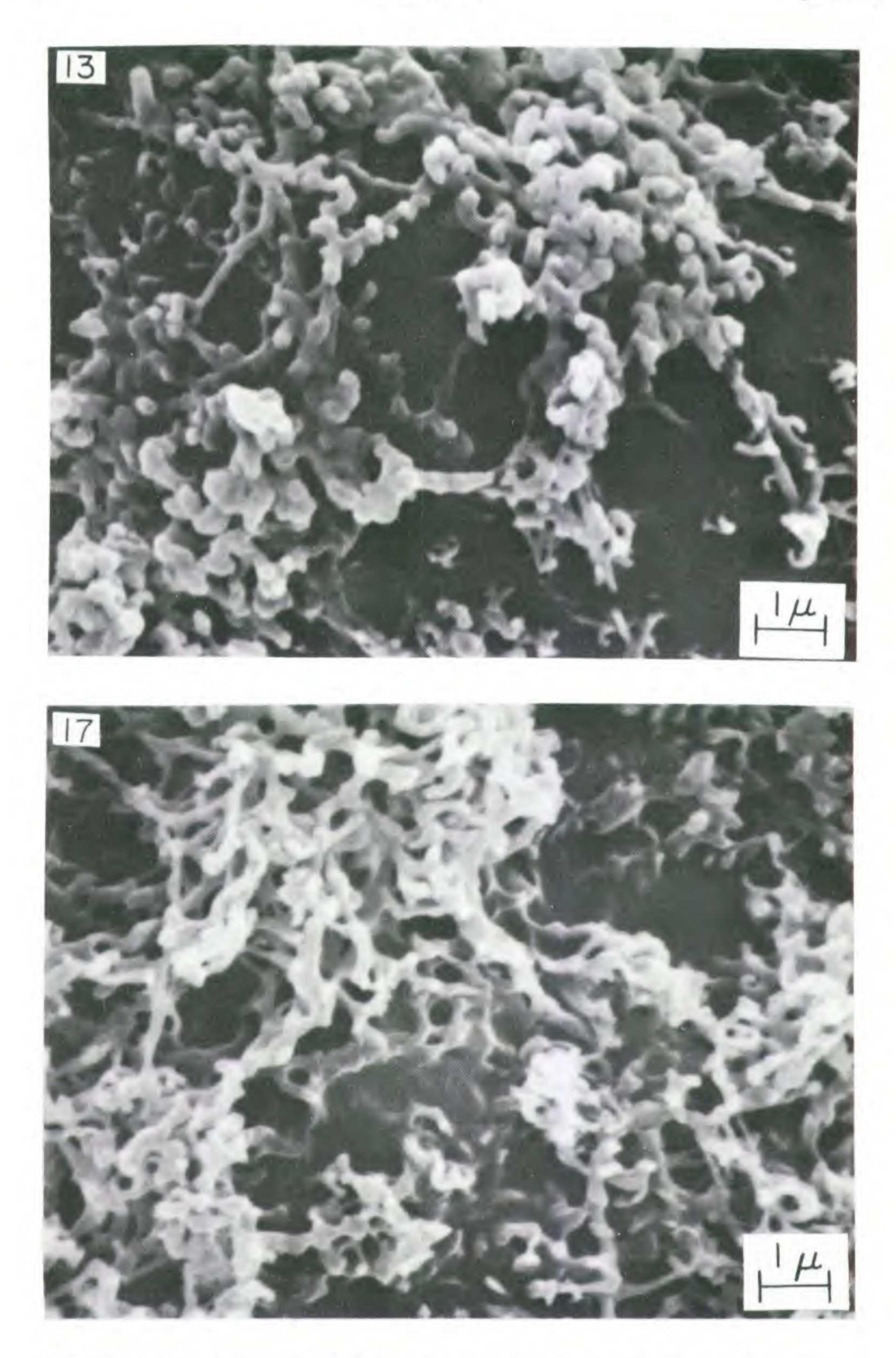
Oxycoccus [Tourn] Hill, Brit. Herb. 324. 1756.

Oxycoccus [Tourn] Adams. Fam. ii. 164. 1763.

Oxycoccus [Tourn] Persoon, Syn. Plant. 1. 419. 1805.

Vaccinium § Oxycoccus [Tourn] A. Gray, Manual 1st ed. p. 260. 1848.

Trailing vines; branches woody, slender, flexible, terete, glabrous or pubescent; leaves alternate, persistent, almost sessile, margin



Figures 13, 17. Glaucescence of the abaxial leaf surface. 13. Wax rodlets, Vaccinium macrocarpon. 17. Wax rodlets, V. oxycoccus.

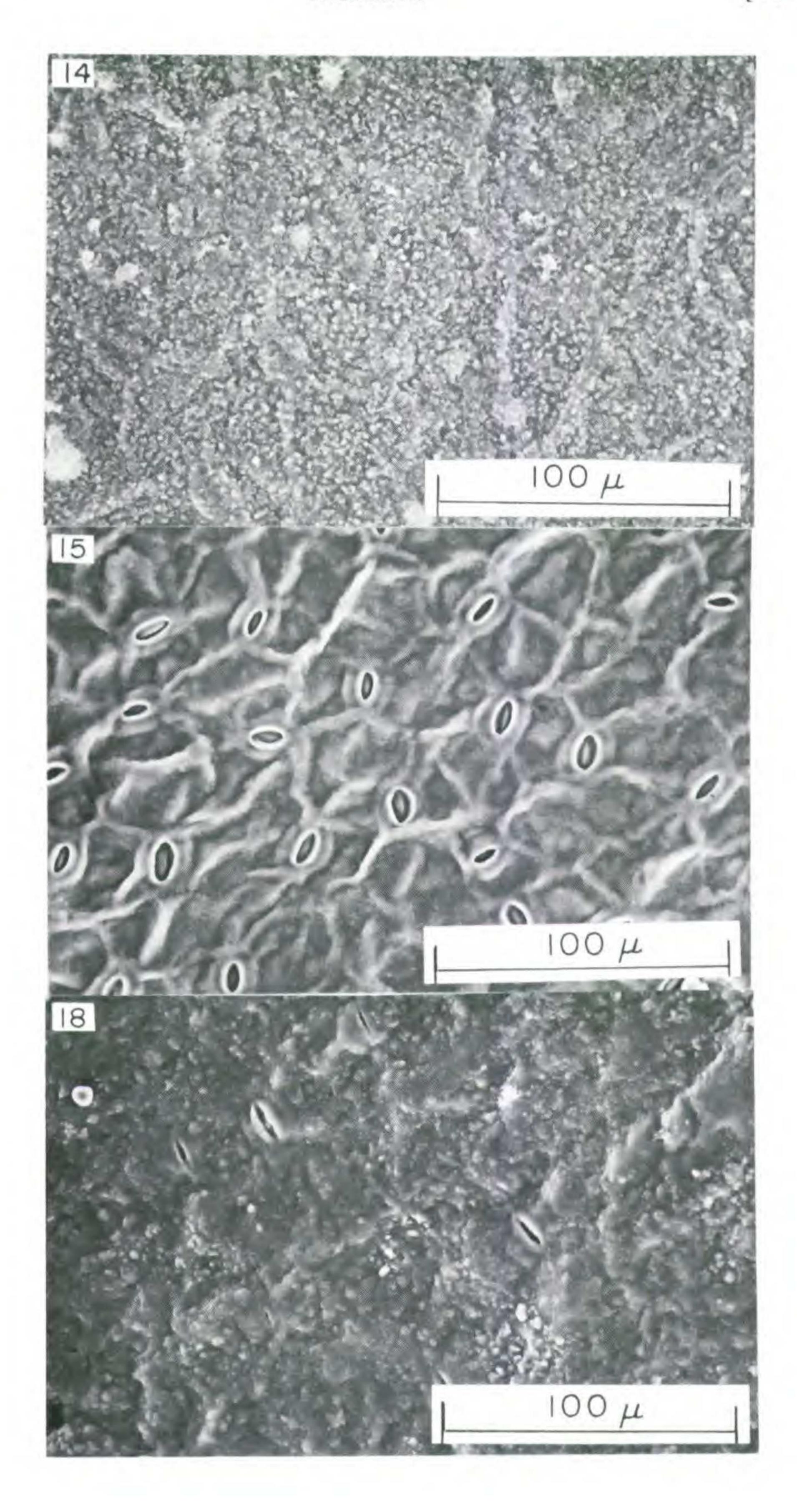
entire; flowers 4-merous, solitary or in small clusters, axillary or apparently terminal, nodding on long slender pedicels; corolla white to dark pink, lobes nearly cleft to the base, strongly recurved at anthesis; anthers 8, awnless but with long slender tubules; ovary 4-celled, fruit a red, several seeded, berry.

KEY TO THE SPECIES

- 1. Vaccinium macrocarpon Aiton, Hort. Kew. ed. i.ii.13. 1789.
 - V. oxycoccus var. oblongifolium Michx. Fl. Bor. Am. 1: 228. 1803.
 - V. oblongifolium (Michx) Hort. ex Dun in D.C. Prod. vii. 576. 1824.
 - V. propinguum Salisb. Prod. 291. 1796.
 - V. macrocarpon f. eburna MacKeever, Rhodora 64: 351. 1962.
 - Oxycoccus macrocarpus (Aiton) Pers. Syn. Plant. 1, 419. 1805.

Trailing woody vine; innovations from axillary buds, frequently erect or ascending, 4-15 cm high. Twigs of the current season terete, golden brown, glabrous, rarely pubescent. Leaves narrowly elliptic, elliptic, rarely oblong; (2)3-4(5) mm wide, (5)7-10(18) mm long; green above, glaucous below with the wax so thick that it frequently obscures the stomata (figures 13, 14, 15); margin entire, scarcely revolute. Flowers borne singly in the axils of reduced leaves at the base of current shoots. Pedicels slender, 2-3 cm long, glabrous or pubescent, bearing a pair of green bracts 1-2 mm wide. Calyx lobes 4, very small. Corolla lobes 4, white to pink, strongly reflexed at anthesis. Stamens 8, filaments usually stiffly pubescent along the margins, rarely entirely pubescent or glabrous; anther sacs awnless, tubules long slender 1-2 mm long; pollen tetrads $32-37~\mu$ in diameter. Style 5-7 mm long, glabrous. Berry red, 9-14 mm in diameter, locules 4, each of which has 2 to 7 large brown seeds (figure 16). Chromosome number 2n = 24.

RANGE: Newfoundland west to central Minnesota south to northern Illinois, northern Ohio and central Indiana and in the Appalachian



Mountains to Tennessee and North Carolina. Its mass centre lies between 40° and 50°N and 70° and 80°W (figure 17). The only report of *V. macrocarpon* occurring north of 50° latitude comes from Sir Joseph Banks (see Lysaght 1971: 69 and 341 where it is argued that the Banksian specimen came from the Bay of Isles (near Cornerbrook) via Wilkinson from James Cook in 1767 rather than from "The Illettes" near Hare Bay in the vicinity of St. Anthony). Aside from the dubious Banksian record, there are in the various herbaria consulted no other specimens extant to support this claim, nor after a diligent 2-day search of the headlands near St. Anthony did I find the plant.

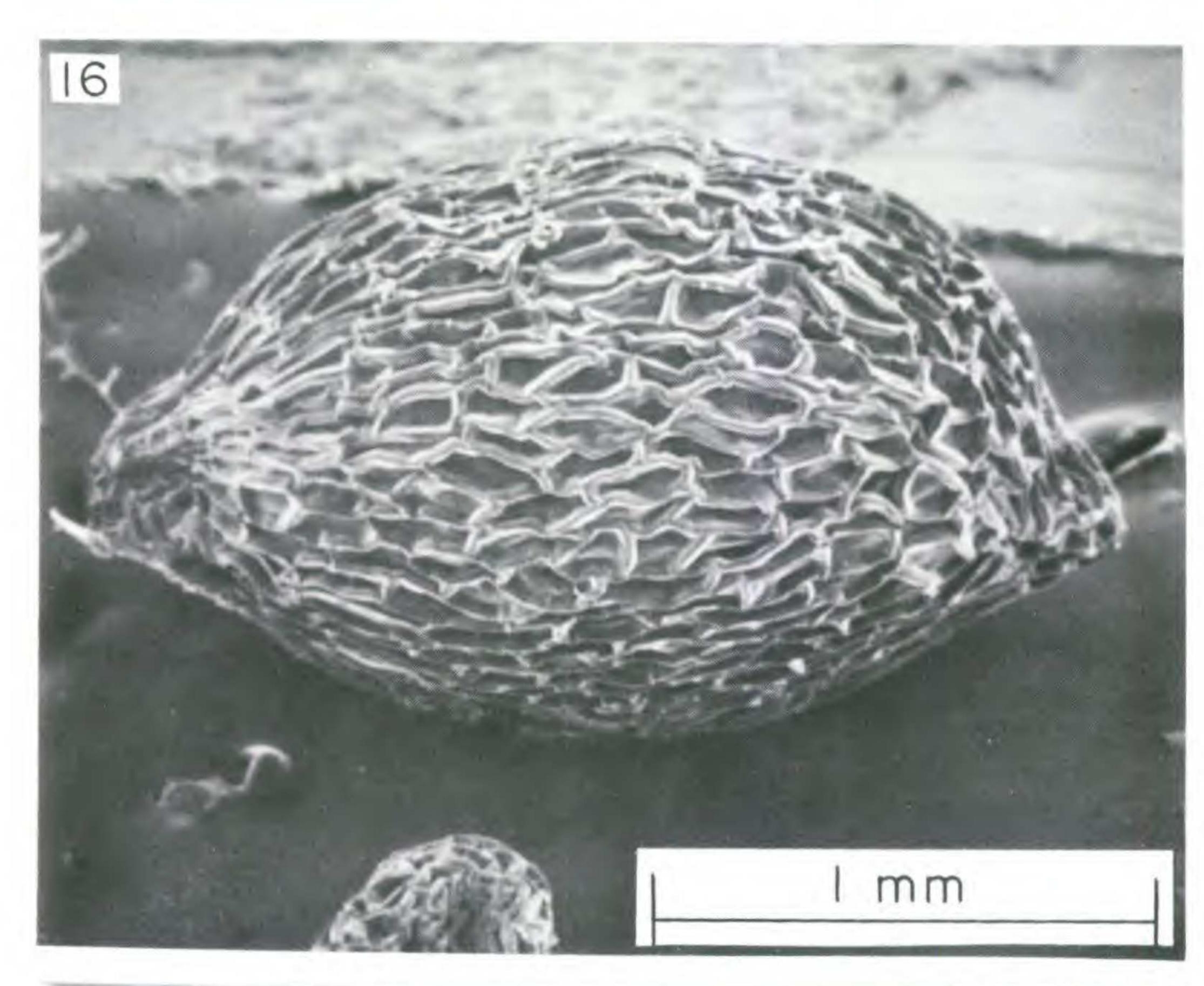
Currently the species is quite rare if not extirpated in Illinois, Ohio, Maryland, North Carolina and Tennessee.

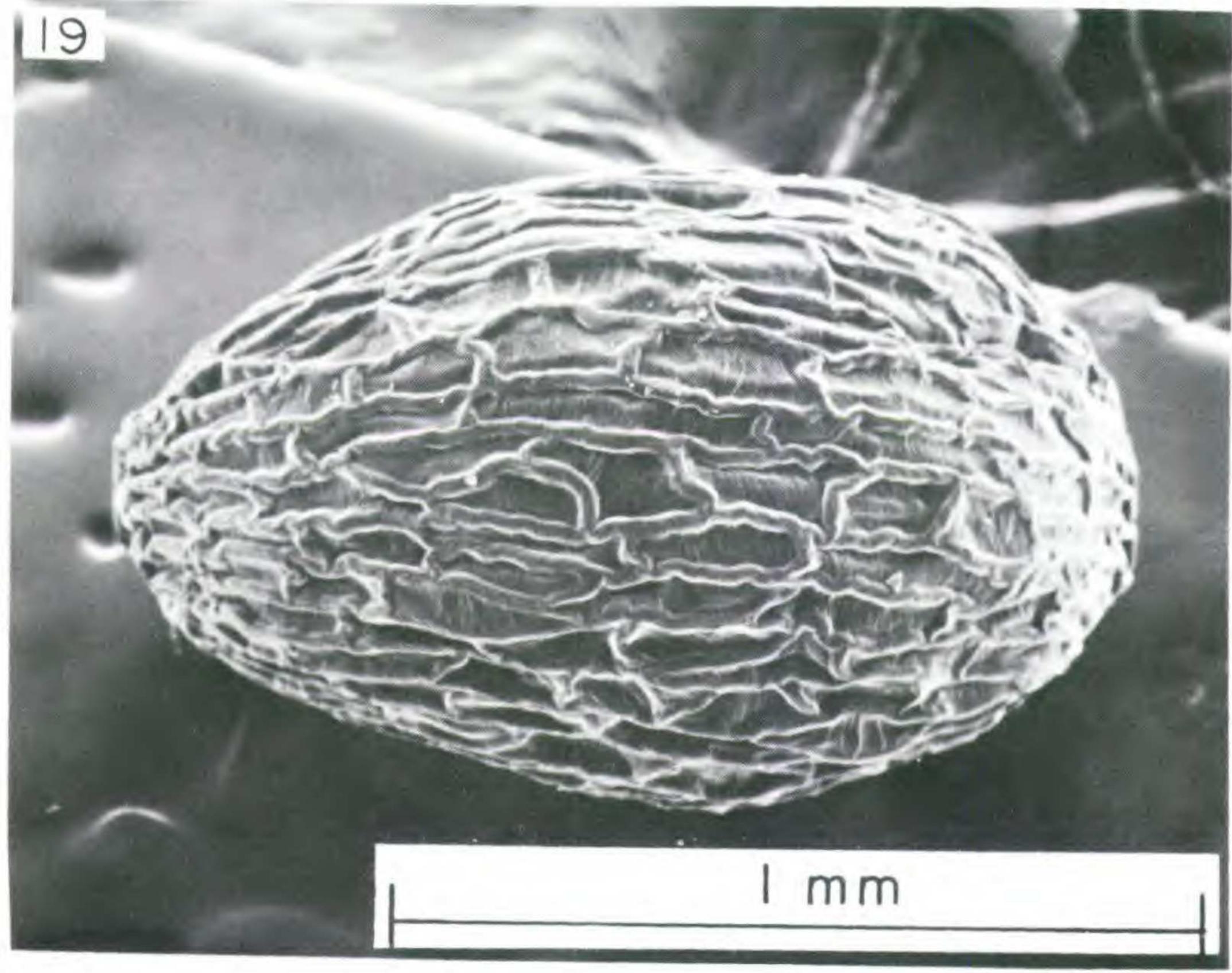
Introduced and adventive along the eastern shore of Maryland (Brown & Brown, 1972) as well as on Lulu Island near Vancouver, British Columbia and several localities in Washington and Oregon. In Europe also the species has been introduced and has become feral in Britain, Germany, Switzerland, and the Netherlands (Popava in Tutin et al. 1972).

Type locality: "Native of North America". Introduced at Kew in 1760 by Mr. James Gordon. Type at BM, seen in 1975. According to Lysaght (1971:341) Aiton's description was based on material from James Gordon as well as on Ehret's plate and not on Banksian material.

HABITAT: open bogs, swamps, mires, wet shores, headlands, and occasionally on poorly drained upland meadows. Occurrence is restricted to acid soils and peat. The pH for 27 soils and peaty substrates tested ranged from a low of 4.8 in bogs to a high of 6.1 in old fields. In open bogs, *V. macrocarpon* is frequently associated with the *Carex-Chamaedaphne calyculata* community at the edge of the floating mat. The species of *Carex* associated with *V. macrocarpon* varies, however: for example, *Carex canescens* (Pers.) Poir in southern New Hampshire (Barrett 1964); *Carex rostrata* Stokes in the Cranberry Glades of West Virginia (Darlington, 1943); *Carex lasiocarpa* Ehrh. in northern Michigan (Gates, 1942); *Carex nigra* (L.) Reichard in Nova Scotia (Hicks, et al., 1968).

Figures 14, 15, 18. Glaucescence of abaxial leaf surfaces. 14, 15. Vaccinium macro-carpon. 14, Glaucescence thick enough to obscure stomata; 15, Removal of glaucescence reveals stomata. 18. V. oxycoccus: glaucescence thick enough to obscure several stomata.





PHENOLOGY: south of 45°N flowering occurs between mid June and mid July and north of 45°N between mid July and mid August. Reproduction is amphimictic, the flowers perfect, protandrous, and entomophilous. Roberts (1978) has found that solitary bees are most efficient at removing pollen from *Vaccinium macrocarpon* flowers, followed by *Bombus* spp. with *Apis mellifera* as the least efficient pollinator; the latter is also inefficient at removing nectar. According to Moeller (1978) in unfertilized flowers the petals turn rosy and persist for several weeks but prompt fertilization causes the petals to drop in a few days.

After pollination, 80-85 days are required for seed set; seed production is a function of pollinator activity. Moeller (1978) found that the plant from which bees were excluded had 6 seeds/berry compared to 12-14 seeds/berry where bees had been permitted to forage. Hall & Aalders (1965) found that berry weight is a function of seed number with each additional seed contributing some 36 mg to total berry weight.

Although the berries turn a deep red in the autumn, and the large seeds are plump and brown, germination studies by Devlin, et al. (1974, 1976) and Devlin and Karczmarczyk (1975, 1977) among others have shown indubitably that seeds harvested in the autumn require heat, high light intensities, ultraviolet, gibberellic acid, or scarification to induce germination. Under natural conditions, the berries hold through winter, and seeds taken from these berries germinate promptly and en masse without pretreatment unless they have been exposed to frequent inundations of salt water during the winter (tables 3 and 4).

2. Vaccinium oxycoccus Linnaeus, Sp. Pl. 351. 1753.

V. palustre Salisb. Prod. 291. 1796.

V. microcarpum (Turcz.) Hook, f. Trans. Linn. Soc. xxiii:334. 1861.

V. microcarpum (Turcz. ex Rupr.) Schmalt. Trudy-Imp.S. Peterb. Obšč. Estestv. 2: 149. 1871.

V. hagerupii (L. & L.) Ahokas, Ann. Bot. Fenn. 8: 255. 1971.

V. oxycoccus var. ovalifolium Michx. Fl. Bor. Am. 1: 228. 1803.

V. oxycoccus var. intermedium Gray. Syn. Fl. N. Am. ed 2.2 pt. 1: 396. 1886.

V. oxycoccus var. microcarpum (Turcz.)

V. oxycoccus var. microphylla (Lange) Rousseau & Raymond, Nat. Can. 79: 82. 1952.

Figures 16, 19. Seeds and seed coats. 16. Vaccinium macrocarpon. 19. V. oxycoccus

- V. oxycoccus f. parvifolia Kurtz. Engl. Bot. Jahrb. 19: 393. 1894.
- V. oxycoccus f. obovatum Lepage, Nat. Can. 81: 259. 1954.
- V. macrocarpon f. dahlei Finlay & Core, Castanea 38: 408. 1973.
- Oxycoccus quadripetala Gilib. Fl. Lituan i:5. 1781.
- O. europaeus Pers. Syn. Plant. 1: 419. 1805.
- O. palustris Pers. Syn. Plant 1: 419. 1805.
- O. vulgaris Pursh, Fl. Am. Sept. 1814.
- O. microcarpus Turcz. ex Rupr. in Beitr. Pfl. Russ. Reich 4: 56. 1845.
- O. oxycoccus (L.) MacM. Bull. Torr. Bot. Club 19: 15. 1892.
- O. intermedium (A. Gray) Rydb. Fl. Rocky Mts. 646. 1065. 1917.
- O. ovalifolius (Michx.) Porsild, Can. Field-Nat. 54: 116. 1938.
- O. hagerupii Löve & Löve, Bot. Not. 114: 40. 1960.
- O. oxycoccus intermedius (A. Gray) Piper, Contrib. U.S. Nat. Herb. 11: 444. 1906.
- O. palustris ssp. microphylla (Lange) Löve & Löve, Univ. Colo. Stud. Biol. Ser. no. 17: 28. 1965.
- O. palustris var. intermedius (A. Gray) Howell, Fl. N.W. Am. 1:413. 1901.
- O. oxycoccus var. intermedius (A. Gray) Farwell, Papers Mich. Acad. Sci. 2: 35. 1923.
- O. quadripetala var. microphylla (Lange) M. P. Porsild, Medd. Grönl. 77: 42. 1930.
- O. palustris var. ovalifolius (Michx.) Seymour, Am. Mid. Nat. 40: 935. 1953.
- O. palustris f. microphylla Lange, Consp. Fl. Grönl 2: 267. 1887.

Trailing wiry woody vine; innovations from axillary buds, often ascending 1-3 cm high. Twigs of the current season terete, very slender, dark brown to red, glabrous to pubescent. Leaves ovate, occasionally elliptic, (1)2-3(5) mm wide, (3)5-6(10) mm long; green above, glaucous below with wax so thick that it frequently obscures the stomata (figures 18, 19); margin entire; frequently revolute and often strongly so. Flowers borne singly in the axils of reduced leaves at the base of current shoots (figure 8), however on most vines the leafy portion of the fertile shoot especially north of 50° latitude does not develop giving the illusion that V. oxycoccus has an inflorescence consisting of a short rachis bearing 1-4 flowers on long slender pedicels (figures 1, 2). Pedicels slender, 2-3 cm long, glabrous to pubescent, bearing (0)2(5) reddish scaly bracts < 1 mm wide. Calyx lobes 4, very small. Corolla lobes 4, white to deep pink, strongly reflexed at anthesis. Stamens 8, filaments usually stiffly pubescent along the margins, occasionally pubescent, rarely glabrous; anther sacs awnless, tubules slender 1 mm long; pollen tetrads 34-46 \mu in diameter. Style 3-4 mm long, glabrous. Berry, at first punctate, later turning deep red, 6-12 mm in diameter, locules 4,

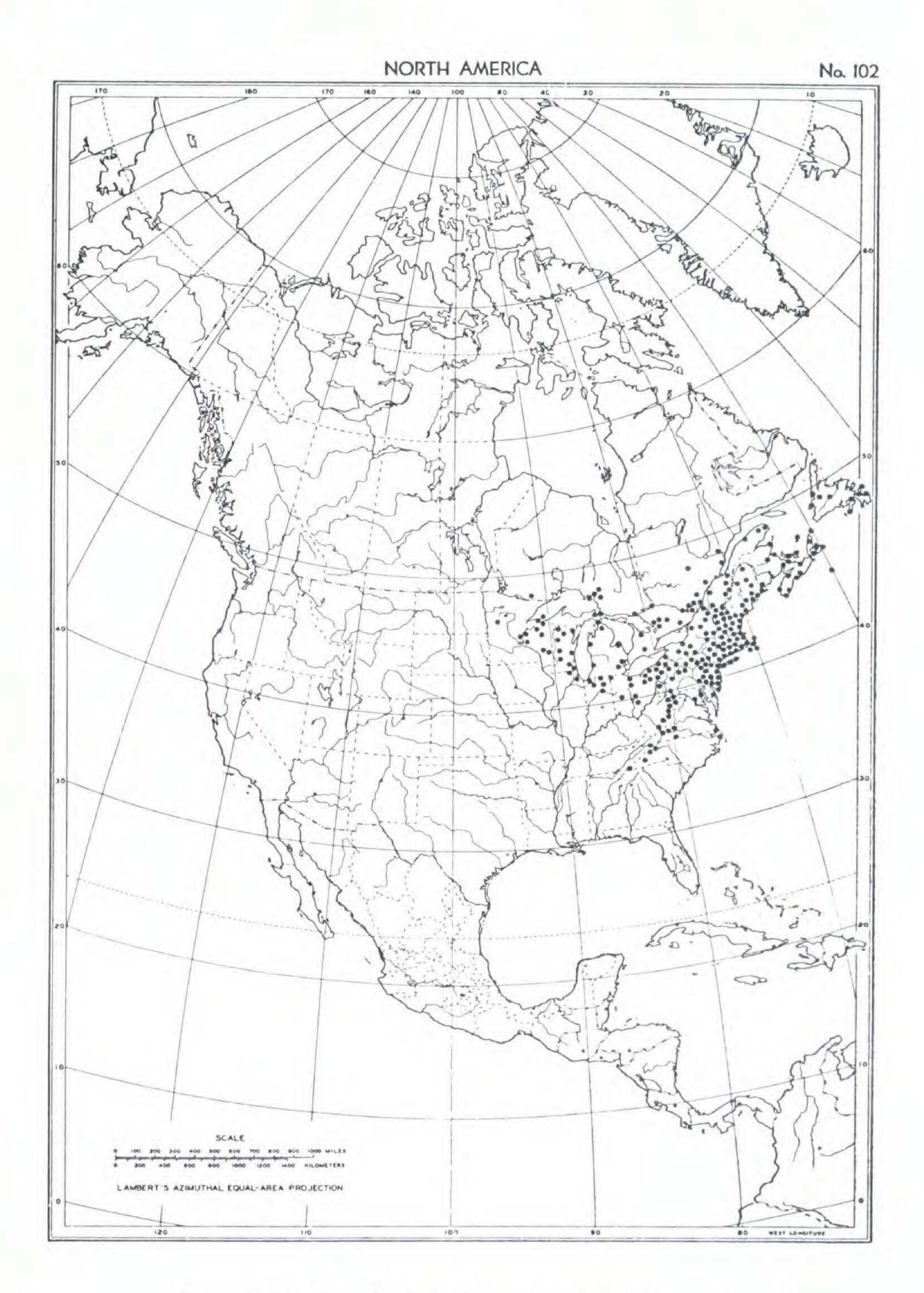


Figure 20. Distribution of Vaccinium macrocarpon.

Coll. #	date	date	# seeds	germination (%)	first radicle emerges (days)	first dicotyledon (days)	first true leaf (days)
NS 1.	27979*	9.XII.80	25	4	30	53	55
NS 4.	27979	"	40	0			
NS 5.	27980	"	48	0			
NS 1.	71079	"	107	0			
NS 2 .	71079	"	87	0			
NS 3 .	71079	"	90	0			
NS 1.	81079	"	141	0			
NS 1.	111080	**	142	2	31	41	54
NS 1.	131080	"	131	0			
NS 2 .	131080	"	124	3	36	44	60
NS 3.	131080	"	131	0			
Ont. 2	. 281080	"	79	82	14	25	31
Ont. 1	. 311080	**	49	100	17	27	33
NS 1 .	1481	1.IV.81	52	96	8	17	23
NS 1.	1481	"	34	76	9	20	25
NS 1 .	1481	"	23	100	9	19	25
NS 2 .	1481	"	60	100	8	17	23

Table 4. Germination characteristics of Vaccinium macrocarpon Aiton.

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NS 1 . 17481	21.IV.81	263	99	9	20	25
NS 2 . 17481	"	230	93	7	20	25
NS 4 . 18481	"	74	94	8	17	24
NS 5 . 18481**	"	414	22	9	17	24
NS 6 . 18481**	"	203	9	7	20	24
NS 7 . 18481**	"	225	1	7	20	24
NS 8 . 18481**	"	207	6	9	21	30
NS 2 . 27481	28.IV.81	6	100	10	21	26
NS 3 . 27481	"	39	100	10	20	25
NS 1 . 201080***	"	167	44	18	30	36
Ont. 1 . 311080***	"	19	78	15	24	30
Ont. 3 . 6581	15.V.81	59	40	11	19	24
Ont. 4.6581	"	24	95	11	21	23

NOTE — *seeds stored in a sealed mason jar at 1°C until sown.

^{**}berries submerged in brackish pools along headlands.

^{***} seeds kept in berries and frozen at -20° C until sown.

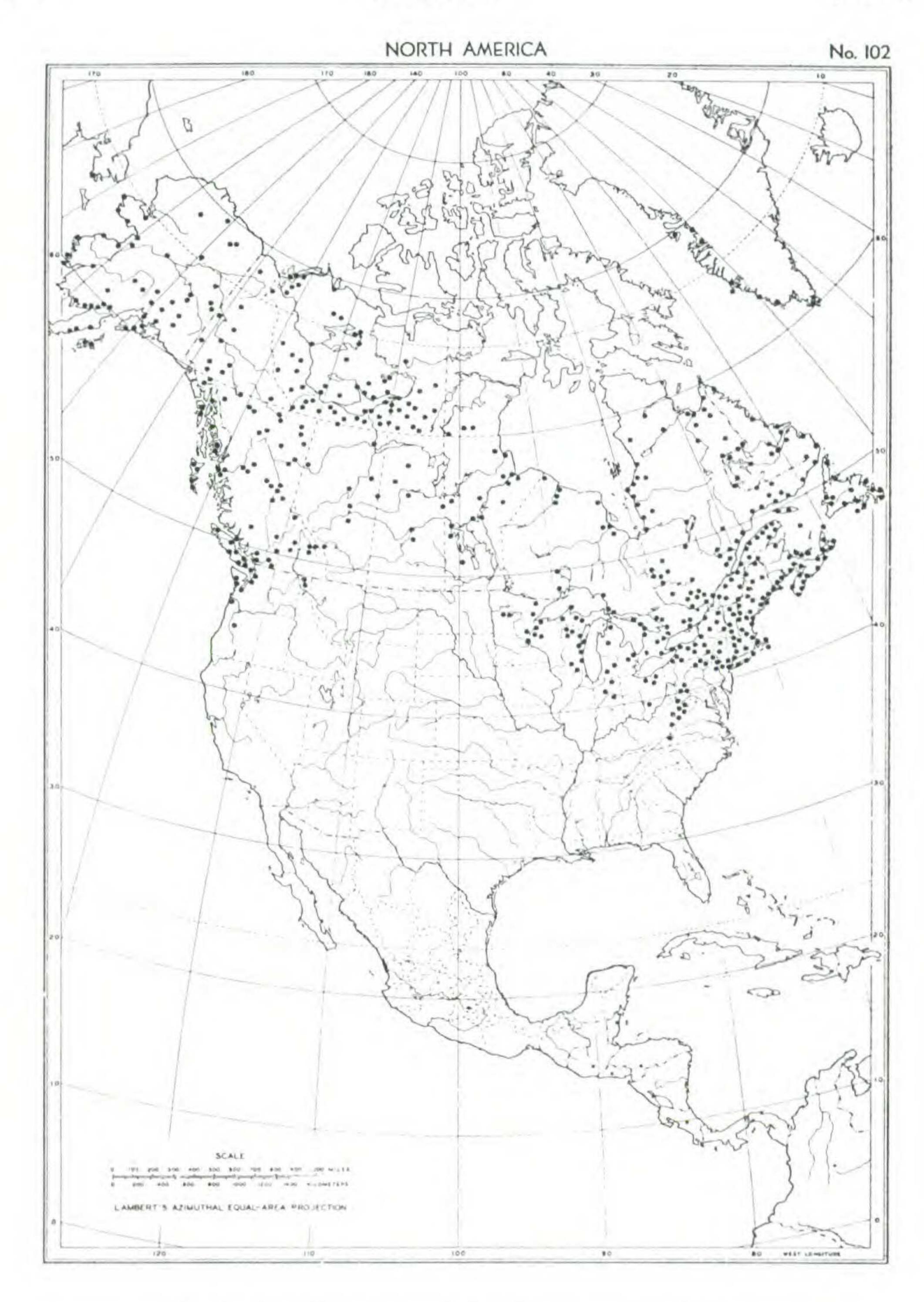


Figure 21. Distribution of Vaccinium oxycoccus.

each of which has 1-4 large brown seeds (figure 20). Chromosome number: 2n = 24, 48, 72.

RANGE: Circumboreal, in North America the species is absent from the Arctic Archipelago including Baffin Island, and extends southwards to Central Oregon in the Cascades and to Virginia in the Appalachians (figure 21).

Type Locality: Sweden, Type at Linn, #497.18, seen in 1975.

HABITAT: half buried in *Sphagnum* hummocks of bogs, the muskegs of the taiga and the low arctic tundra. This habitat is best described as oligotrophic with low pH (2.9–3.8), few exchangeable cations (Grandtner, 1960) and little available nitrogen and phosphorus (Small, 1972).

PHENOLOGY: Anthesis occurs from mid-May to mid-June in New Jersey, eastern New York, Connecticut, Massachusetts, south-eastern Ontario, Washington and southern British Columbia; from mid-June to mid-July in the Appalachians, Pennsylvania, New Hampshire, Maine, Vermont, northern New York, central Ontario, adjacent Quebec and the Maritimes as well as the West in that area west of 100° longitude and south of 65°N. In the remainder of the continent the species flowers from mid-July to mid-August. Reproduction is amphimictic, the flowers perfect, protandrous and entomophilous. Bombus spp. and solitary bees are the most frequent pollinators. After pollination, 85–90 days are required for seed set in New England, the Maritimes and southern Ontario and Quebec, but only 35–45 days in the low arctic regions. Seed set and seed weight are invariably less than in V. macrocarpon even where the two species share the same bog (table 2).

As in Vaccinium macrocarpon, V. oxycoccus berries hold over winter and are dispersed by water, birds, and mammals in early spring. As in V. macrocarpon, seeds collected in the spring germinate most readily (table 5), except that the rate of germination is significantly higher in V. oxycoccus in both the vernal and autumnal trials. Moreover berries collected in late October and early November contain seeds ready to germinate so whatever the after ripening requirement may be, it has been met before the actual onset of winter in V. oxycoccus but not in V. macrocarpon, which is to be expected since it flowers 3 weeks later therefore also sets seeds 3 weeks later than V. oxycoccus.

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Coll.	collec		# seeds	germination (%)	first radicle emerges (days)	first dicotyledon (days)	first true leaf (days)
NS 1	. 16979	9.XII.80	36	0			
NS 2	. 16979) "	65	0			
NS 3	. 16979)	53	3	19	33	50
NS 2	. 27980)	59	5	17	33	59
NS 3	. 27980)	50	0			
NS 2	. 81079)	33	0			
NS 3	. 81079)	57	0			
NS 2	. 91079	, , ,	63	3	19	29	36
NS 6	. 13108	0 "	75	2	21	32	39
NS 7	. 13108	0	68	4	27	33	44
NS 1	. 14108	0	19	5	21	33	39
P. Q. 1	. 26108	0	39	79	14	25	29
Ont. 1	. 28108	0	26	26	17	30	36
P. Q. 1	. 21180	,,,	174	96	14	25	29

Table 5. Germination characteristics of Vaccinium oxycoccus L.

NS 1 . 18481	21.IV.81	62	96	9	20	25
NS 2 . 18481	"	55	100	9	20	29
NS 3 . 18481	"	267	89	9	20	29
NS 1 . 27481	"	24	100	12	21	30
P.Q. 1 . 261080**	.,,	52	98	16	22	27
P.Q. 1 . 4581	15.V.81	63	99	11	19	23
P.Q. 2 . 4581	"	185	96	10	19	23
Ont. 1 . 6581	"	214	83	11	19	23
Ont. 1 . 6581	"	65	84	1 1	19	24
P.Q. 1 . 12581	"	16	87	11	19	24
P.Q. 2 . 12581	"	106	100	7	16	22

NOTE — *seeds stored in a sealed mason jar at 1°C until sown.

**seeds kept in berries and frozen at -20°C until sown.

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APPENDIX I. LOCATION OF SAMPLING SITES

*Chromosome number determined for one or more plants.

- 1. Jet, of Webbs Mill Brook and SR539, Ocean County, New Jersey; mire; V. macrocarpon.
- 2* Mast Way, Lee, Strafford County. New Hampshire; bog; V. oxycoccus (n = 24) 2 plants.
- 3. Quoddy Head, Washington County, Maine; hummocks on high moor; V. oxycoccus.
- 4. Drakes Island, Rachel Carson Wildlife Refuge, York County, Maine; red maple swamp; V. macrocarpon.
- 5* Mud Lake, 1 km west of Black River Lake, Kings County, Nova Scotia; bog; V. oxveoccus and V. macrocarpon (n = 12) 6 plants.
- 6* 4 km E of Kingston along Hwy. 1, Kings County, Nova Scotia; boggy depressions; V. macrocarpon (n = 12) 1 plant.
- 7. Little Lorraine, Wild Cove, Cape Breton County, Nova Scotia; rocky head-lands; V. macrocarpon.
- 8. Leap Frog Lake, Port Maitland, Yarmouth County, Nova Scotia; boggy margin; V. oxycoccus.
- 9. 8 km west of Birchtown along Hwy. 3, Shelburne County, Nova Scotia; raised bog and boggy barrens; V. oxycoccus.
- 5 km N of exit 46 along Hwy. 104, Richmond County, Cape Breton Island, Nova Scotia; raised bog; V. oxycoccus.
- 11. 1.5 km N of West Dover along Hwy. 333, Halifax County, Nova Scotia; boggy barrens; V. oxycoccus.
- 12. French Mountain, Cape Breton Highlands, Inverness County, Nova Scotia; extensive high moor; V. oxycoccus.
- 13. Red Head, Port Maitland, Yarmouth County, Nova Scotia; mire; V. oxycoccus; headlands, V. macrocarpon.
- 14* 4 km west of West Branch, Pictou County, Nova Scotia; abandoned, poorly drained Festuca ovina meadow; V. macrocarpon (n = 12) 1 plant.
- 15* Portuguese Cove Headlands, Halifax County, Nova Scotia; headlands; V. macrocarpon (n = 12) 2 plants; boggy depressions, V. oxycoccus (n = 24) 1 plant.

- 16* Kennington Cove, Cape Breton County, Nova Scotia; raised bog, V. oxycoccus (n = 24) 2 plants; headlands, V. macrocarpon (n = 12) 5 plants.
- 17. 2 km SW of Bonavista, Massive headlands, Newfoundland; boggy depression between headlands; V. oxycoccus.
- 18. RT185 at P.Q. N.B. border, Temiscouata County, Quebec; spruce woods and extensive bogs; V. oxycoccus (n = 24).
- 19* Villeroy, Route 20, Sortie 158, Lotbiniere County, Quebec; raised bog; V. oxy-coccus (n = 24) 3 plants, V. macrocarpon.
- 20. Along SR8 at Graphite, Warren County, New York; lake margin; V. macro-carpon.
- 21. Westport Bog, 4 km NE of Westport, Leeds County, Ontario; bog; V. oxycoc-cus, V. macrocarpon.
- 22* Byron Bog, suburban London, Middlesex County, Ontario; bog; V. oxycoccus (n = 24) 3 plants; V. macrocarpon (n = 12) 1 plant.
- 23. 1 km W of Heart Lake, near Snelgrove, Peel County, Ontario; bog; V, macrocarpon.
- 24. Mer Bleue, beyond Borthwick Road, Carleton County, Ontario: raised bog; V. oxycoccus, V. macrocarpon.
- 25* Hebert Bog, Upper Rock Lake, Frontenac County, Ontario; bog; V. oxycoccus (n = 24) 6 plants; V. macrocarpon (n = 12) 4 plants.
- 26. Fraser River Delta at Richmond Rd #5 and the CNR right-of-way, Lulu Island, British Columbia; disturbed raised bog; V. macrocarpon.

APPENDIX II

Citation of Specimens

Greenland. Ameralik Fj. Ameragdla Arm. Equaluit, 64°09'N, 50°22'W, A. E. Porsild 8406 in 1941 (CAN); otu 2. Amitsuarssuk, 60°08'N, 44°45'W, Carlo Hansen, Lars Kliim-Nielson, and Benjamin Ølgaard 67–408 in 1967 (CAN); otu 3. Frederikshaab, 62°, J. Eugenius in 1928 (CAN); otu 47. Godthaab Fj. S. point of Sadlen Island, A. E. Porsild 12000 in 1942 (CAN); otu 42. Godthaab Fj., Qornoq Island, 64°30'N, 51°05'W, A. E. Porsild 8698 in 1942 (CAN); otu 41.

CANADA.

Alberta. Anzac, S.E. tip of Gregoire Lake, S.E. of McMurray, M. G. Dumais and K. Anderson 2692 in 1968 (ALTA); OTU 9. 1/2 mi. S. of Ma-Me-O Beach, G. H. Turner MD. 8332 in 1953 (ALTA); OTU 8. Primrose Lake, 6 mi S of tip of lake, M. G. Dumais and C. G. Rankin 1287 in 1967 (ALTA); OTU 7.

British Columbia. Cape Beale, Lake Kihha, S. Hartwell 62503 (UAC). Georgie Lake, Port Hardy, J. Hett and W. Armstrong 303 in

1964 (UVIC). Lulu Island, Vancouver, J. W. Eastham 11,434 in 1944 (ALTA). Wolverine Range, near Manson Creek village, N. of Ft. St. James, 55° 40′N, 124° 22′W, J. A. Calder, D.B.O. Saville and J. M. Fergusson 13690 in 1954 (DAO).

Nova Scotia. Colchester County, Earltown, A. R. Prince 206 in 1927 (ACAD); OTU 5. St. Paul Island, J. S. Erskine 53,693 in 1953 (DAO).

N.W.T. Dumpy Lake, near Eldorado Mine, Port Radium, E end of McTavish Arm, Great Bear Lake, 66°05'N, 118°02'W, Hansford T. Shacklette 2766 in 1948 (CAN); OTU 43. Grassy Island, Thelon River, John S. Tener 259 in 1952 (CAN); OTU 44. Hornby's Bend. Thelon River, John S. Tener 258 in 1952 (CAN); OTU 45. Keewatin, mouth of Windy River, F. Harper 2347 in 1947 (CAN); OTU 46. MacKenzie Lowlands, Liard R. Valley, 10 mi. N of B.C. boundary, W. W. Jeffrey 84 in 1959 (CAN).

Ontario. De Grassi Pt., Lake Simcoe, E. M. Walker in 1894 (TRT). Durham County, Newtonville Bog, J. C. Krug and J. E. Purchase 484 in 1963 (TRT). Grey County, Stewart Lakes, 44°23′N, 80°55′W, G. R. Thaler 182 in 1965 (TRT). Holland Swamp, near Newmarket, W. C. McCalla in 1896 (ALTA); OTU 10. London and Parry Sound, T. J. W. Burgess and D. Burgess in 1880 and 1881 (TRT). Mador, Snake Lake, Hastings in 1907 (TRT). Middlesex, Byron Bog, W. W. Judd in 1956 (TRT). N.W. of Nuelton Lake, mouth of Windy Lake, S.W. Keewatin, Francis Harper 2347 in 1947 (CAN). Wellington County, Brisbane, 3/4 mi. S. just off Hwy. 24, 43°44′N, 80°05′W, G. R. Thaler 119 in 1965 (TRT). Wellington County, Puslinch, J. J. Stroud in 1939 (TRT). Wentworth County, 1 mi. S.E of Copetown, J. H. Soper and J. K. Shields 4735 in 1950 (TRT). York County, Holland R. Marsh, Roy F. Cain in 1930 (TRT). York County, Pottageville, W. R. Watson 2668 in 1926 (TRT).

Yukon. Halfway Lakes, 15 mi. N of Mayo, 63°48'N, 135°48'W, W. A. Calder, J. M. Gillett and D. A. Mitchell 4156 in 1949 (DAO). Jensen Flats, 6 mi. on rd. to Paris fr. Granville, 63°42'N, 138°33'W, J. A. Calder and L. G. Billard 3163 in 1949 (DAO). Peavine Camp, tributary of Porcupine River, 65°48'N, 138°35'W, J. A. Calder and J. M. Gillett 26243 in 1960 (DAO).

UNITED STATES

Alaska. Eagle River, near Juneau, J. P. Anderson 6351 in 1940 and 1941 (DAO). Lake Spenard, Anchorage, Dutilly, Le Page and

O'Neill 20,274 in 1947 (DAO). 2 mi. N of Seward-Kenai-Anchorage rd. junction, Kenai Peninsula, 60° 34′N, 149° 35′W, J. A. Calder 5757 in 1951 (DAO). Naknek, W. B. Schofield 1951 in 1952 (DAO). Sterling Hwy. between Kasilof and Homer, Kenai Peninsula, 60° 20′N, 151° 16′W, J. A. Calder 5417 in 1951 (DAO).

Maine. Aroostook Co., Crystal, A. R. Hodgdon and William Countryman 19285 in 1971 (NHA). Cumberland Co., Perley Pond, Sebago, M. L. Fernald, Bayard Long and A. H. Norton 11854 in 1916 (NHA). Washington Co., on hwy. 191 near S.W. corner of Cathance Lake, Edw. & Susan Johnson 279 in 1970 (NHA). Washington Co., Jonesport, C. A. Cheever in 1905 (NHA).

New Hampshire. Carroll Co. Mystery Pond, Ossipee, A. R. Hodgdon and T. Marsdon Jones 3376 in 1939 (NHA). Carroll Co. Ossipee, Heath Pond Bog, Irene M. Storks 328 in 1978 (NHA). Carroll Co. Tamworth, A. R. Hodgdon, Anthony J. Hodgdon, and Alec Lincoln 7819 in 1954 (NHA). Coos Co. Pittsburg, A. R. Hodgdon and P. Allen, et al. 11941 in 1960 (NHA). Grafton Co. Heath Pond Bog, Paul Barrett and A. R. Hodgdon 15534 in 1965 (NHA). Hillsborough Co., Greenfield, Hogback Pond, Greenfield State Park, A. R. Hodgdon, Peter Allen, Henry Baldwin 12724 in 1963 (NHA). Rockingham Co. Kingston Cedar Bog Pond, A. R. Hodgdon and F. L. Steele 20002 in 1973 (NHA). Rockingham Co. Kingston Jct Rt. 125 and Rt. 111, Garrett E. Crow 2284 in 1976 (NHA). Strafford Co. Madbury, Barbadack Pond, Lee Rodrigues and A. R. Hodgdon 12415 in 1962 (NHA). Strafford Co. Barrington, near Winkley Pond, A. R. Hodgdon and H. A. Giddings 4612 in 1943 (NHA). Strafford Co. Lee, A. R. Hodgdon and H. Clapp 3383 in 1940 (NHA).

Vermont. Windham Co. Whitingham, "floating Is." anchored ericaceous bog in Lake Sedoga S. of Wilmington, A. R. Hodgdon 19954 in 1973 (NHA).

FINLAND

South Savo, Sulkava, Partalansaari, Auvila, S. W. shore of Lake Kikolampi, Marjatta Isoviita in 1976 (ALTA).